

High Risk Behaviors in Marine Mammals: Linking Behavioral Responses to Anthropogenic Disturbance to Biological Consequences

Terrie M. Williams
Center for Ocean Health- Long Marine Lab
Department of Ecology and Evolutionary Biology
100 Shaffer Road
University of California-Santa Cruz
Santa Cruz, CA 95060
phone: (831) 459-5123 fax: (831) 459-3383 email: williams@biology.ucsc.edu

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LONG-TERM GOALS

The proposed project focuses on the physiological costs and potential risks of three common responses by cetaceans to oceanic noise, 1) high-speed swimming, 2) elevated stroke frequencies, and 3) rapid ascent from depth. By combining data from previous studies as well as from the proposed experiments, we will provide the first comprehensive evaluation of biological safety zones for diving marine mammals. In this way we intend to identify those marine mammal species or specific attributes of each species that are associated with susceptibility to acoustically mediated disturbance and tissue damage. Furthermore, by identifying high risk and low risk behaviors, and the specific triggers for tissue injury and cardiac instability, we will accomplish the overall objective of improving the protection of marine mammals during naval operations.

OBJECTIVES

We are testing the hypothesis that extreme behaviors requiring marine mammals to perform outside of preferred physiological states represent a graded risk to metabolic and cardiovascular homeostasis during diving, and account for species-specific vulnerabilities to anthropogenic perturbation. Four specific aims are being addressed:

1. Determine physiological costs and risks of high speed behaviors

Recognizing the importance of the mammalian flight response to novel stimuli, we are conducting the first evaluation of the metabolic consequences of high speed performance during diving in a cetacean, the bottlenose dolphin (*Tursiops truncatus*). Indices of dive capacity (aerobic duration, recovery rate, and number of strokes and heart beats in relation to aerobic dive limits) will be defined.

2. Evaluate species-specific costs and cardiovascular risks of high stroke frequency responses

Because the movement of gases (oxygen, carbon dioxide, nitrogen) and metabolic byproducts (lactic acid) depends on heart rate, and the latter is correlated to stroke frequency in marine mammals, we are examining how high performance stroke mechanics (frequency and amplitude) may be linked to tissue

injury via cardiovascular performance during submergence. Neuro-protection through globin deposition and capillarity at the tissue level as well as the impact of high intensity performance on heart rate will be compared for swimming and diving specialists including dolphins, beluga whales, narwhals and foraging Weddell seals.

3. Determine risks and safety zones for rapid ascents by marine mammals

The effects of high speed ascents on cardiovascular stability in cetaceans are being examined by assessing patterns in inter-beat intervals and incidence of arrhythmias from ECGs recorded continuously during vertical sprints by bottlenose dolphins. Comparable tests conducted on trained dolphins in pools and open water as well as on wild narwhals will enable us to identify “safety zones” for cardiac stability related to depth and segment of the dive for different cetacean species.

4. Integrate energetic and cardiac risk factors for development of 3-D safety zones for diving marine mammals

To promote the incorporation of data from these studies into US Navy environmental programs we intend to develop several predictive models integrating depth with physiological capacity and stability for different classes of diving marine mammals. Model elements include allometric relationships for stroking costs, aerobic dive limits, types of neuro-protection (globin deposition, capillarity), and cardiac risk factors that will be mapped on 3-D physical attributes (e.g., home range, hydrostatic pressure) of the marine environment.

Overall, successful completion of the proposed project will allow us to define the major non-disease related factors leading to the observed species-specific propensity for stranding, and enable the development of scientifically-based, environmentally sensitive schedules for naval operations.

APPROACH

This study uses two approaches to determine the relative susceptibility of different marine mammal species to acoustically mediated trauma, 1) tissue/whole animal/physiological exercise assessments to determine the impact of behavioral and environmental challenges to the dive response, and 2) physiological mapping to predict when during a dive and where in the water column marine mammals may be especially vulnerable to anthropogenic perturbation. The following methods will be used:

Part I.

Physiological costs of high speed behaviors

To determine if high speed behaviors impede diving performance by cetaceans, we are conducting measurements of diving energetic costs for bottlenose dolphins using open-flow respirometry. Tests will be conducted on trained dolphins both in pools of varying in depth. We will determine the effect of swimming speed, dive duration, and physical exertion on overall diving costs and recovery. Post-dive blood lactate will be used to evaluate the combination of behaviors that cause the animals to surpass aerobic limits.

Species-specific cardiovascular/high stroke frequency responses

We are using a comparative approach to examine cardiovascular adaptations at both the tissue and whole animal levels that safeguard marine mammals against hypoxic tissue damage when exercising. We will determine the relationship between the deposition of resident globins (neuroglobin,

cytoglobin) in the brain, circulating globins (hemoglobin) in the blood, and vascularization for oxygen delivery via the capillaries in swimming and extreme diving specialists including beaked whales, melon-headed whales, narwhals, Weddell seals, and elephant seals. At the whole animal level we will evaluate the interrelationship between stroke mechanics (frequency and amplitude), heart rate variability, and submergence as trained and wild cetaceans wearing a custom-designed ECG-stroke frequency instrument transition from routine preferred levels of exercise to high intensity performance both near the water surface and at depth. Small and large cetacean species will be compared to determine the effects of body size on responses.

Team members include specialists in marine mammal morphology/tissues (M. Miller, CA Dept. Fish and Game; R. Dunkin, UCSC), globin chemists (D. Kliger and R. Goldbeck, UCSC), molecular biologists (M. Zavanelli, UCSC), physiologists (T.M. Williams, D. Casper, N. Thometz and S. Noren, UCSC), and animal behaviorists (T. Kendall and B. Richter, UCSC).

Part II.

Risks and safety zones for rapid ascents by marine mammals

Here we test hypotheses concerning behavioral, physiological and environmental factors leading to cardiac arrhythmias and physiological instability in diving marine mammals. Specifically, we will determine which factors or combination of factors act as the primary instigator of cardiac variability that has been observed for diving marine mammals. Sprint tests will compare the sequential change in inter-beat interval (IBI) of the heart in trained bottlenose dolphins during underwater and surface performances. We will deploy our custom designed ECG-stroke monitor on exercising and diving animals to continuously and simultaneously monitor cardiac and kinematic responses. We will identify, 1) the incidence of arrhythmias, 2) triggers for cardiac anomalies, and 3) the segments of dives (descent, bottom, ascent) associated with cardiac instability.

3-D safety zones for diving marine mammals

To maximize the effectiveness of our data we will develop several quantitative models based on US Navy Decompression Tables that incorporate time at depth, oxygen limitations, nitrogen exchange and ascent rate to delineate the bounds of safe diving conditions for humans, as well as ecological home range models that take into account external environmental and internal animal characteristics to predict movement paths. The resulting stochastic dynamic state variable (SDSV) model will be parameterized with physiological costs and risk factors determined during this project and our previous research. Simulations using the models will be used to develop a physiological-based framework for understanding preferred diving behaviors and depth selection by different marine mammal species, and the effect of anthropogenic perturbation on those behaviors. To broaden the application from individual level to population level consequences, we will provide the input parameters for our models to research groups involved in the construction of Population Consequences of Acoustic Disturbance (PCAD) models.

Team members for this part of the program include physiologists (T.M. Williams, UCSC; R. Davis, Texas A&M University), animal behaviorists (T. Kendall and B. Richter, UCSC; P. Berry, EPCOT; Mads Peter Hyde-Jørgensen, Greenland Institute of Natural Resources),) and ecological modelers (R. Dunkin and T. Tinker, UCSC).

WORK COMPLETED

This project began July 2013 with a first year focus on developing the infrastructure for the program. To date this has included, 1) obtaining federal and institutional permitting for all animal use protocols, 2) preliminary assessment and modification of instrumentation for ECG monitoring in comparative marine mammal species, 3) coordination of biomechanics data sets for free-ranging cetaceans with collaborating investigators, 4) training for bottlenose dolphin performance studies, and 5) completion of ECG variability analysis for free-ranging dolphins and seals that form the foundation for this project.

Last year we developed and successfully deployed highly sensitive, kinematic-linked ECG recorders on a wild, deep diving cetacean, the narwhal (*Monodon monoceros*), and begun exercise trials with a shallow diving cetacean, the bottlenose dolphin. Importantly, new collaborations with Mads Peter Heide-Jørgensen (Greenland Institute of Natural Resources), Susanna Blackwell (Greenridge Sciences Inc.), Ari Friedlaender (Oregon State University) and Brandon Southall (SEA, Inc., and UCSC) have facilitated comparative kinematic and cardiac analysis for a wide variety of cetacean species for this project. In addition to the physiological studies, tissue level protocols and preliminary work on comparative brain capillarity began during this year and managed by a new post-doctoral researcher, Nicole Thometz. This year we conducted a comprehensive study on the ECG responses of free-ranging narwhals that now include 7 animals and deployment records of up to 50 hours in duration. Work on trained dolphins and on brain samples is ongoing for the development of detailed kinematic-cardiac-metabolic models and a library of brain capillary densities for swimming and diving marine mammals.

RESULTS

Following redesign of the electrode system for the UFI kinematic ECG recorder last year we continued our work on free-ranging, deep diving cetaceans (Fig. 1). In collaboration with Mads Peter Heide-Jørgensen we monitored cardiac variability in resting and diving adult narwhals ($n = 4$) in Scoresby Sound, East Greenland during 2015. Cardiac responses of the animals were highly variable and related to the physiological state of the individual, suggesting a new metric for evaluating normal and acute stress responses for this species. New kinematic analyses of whole body kinematics and accelerometry using Overall Dynamic Body Acceleration (ODBA) for phocid seals, and shallow and deep diving cetaceans indicate a complex interaction between ODBA and stroke frequency that is dictated by the propensity for non-propulsive maneuvers by marine mammals. We are currently evaluating the impact of this on metabolic models for diving. Lastly, preliminary evaluations comparing capillary densities for the cerebral cortex of terrestrial (cougar), transitional (sea otter), and marine (bottlenose dolphins) indicate a gradient in capillarity corresponding to the globin deposition and breath-hold capability of the species (Fig. 1B). These data concerning the intrinsic and extrinsic factors affecting cardiac and metabolic responses are currently being used in development of risk models for marine mammals.

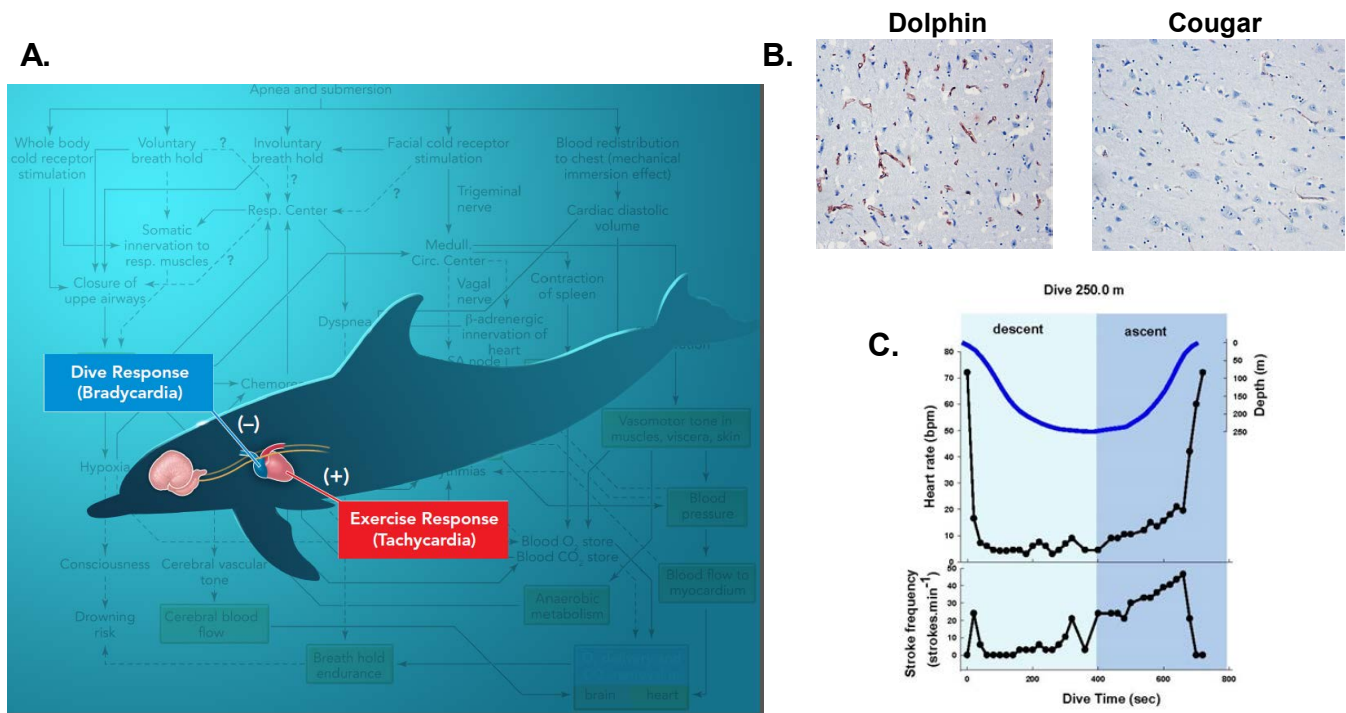


Figure 1. Integrating the anatomical-physiological-behavioral capacity of diving cetaceans. Panel A illustrates the complexity of the signals impacting cardiac function in diving cetaceans with two main opposing signals during submerged exercise (from Williams et al. 2015, Physiology). Panel B shows the relative difference in capillary density (red stained areas) in the cerebral cortex of bottlenose dolphins (left) and cougars (right). In panel C, the changes in heart rate in relation to depth (upper dark blue line), dive duration (upper black line) and stroke frequency (lower black line) are presented for a 250 m dive by free-ranging narwhals.

IMPACT/APPLICATIONS

This study will provide one of the first comparative evaluations of biological safety zones for diving marine mammals. In this way we intend to provide data that will help mitigate current misunderstandings regarding lethal and sub-lethal impacts of anthropogenic disturbance on marine mammals by providing a comprehensive understanding of how animals specialized for swimming or diving maintain physiological homeostasis in the face of perturbation. In a novel series of exercise experiments using unique instrumentation on trained and wild cetaceans we will define the energetic costs and physiological risks associated with exercising at depth. By combining data from ongoing and previous studies as well as from the proposed experiments, we will identify those marine mammal species or specific attributes of each species that lead to susceptibility to acoustically mediated disturbance and tissue damage. This will subsequently allow us to achieve our overall goal of enabling Navy personnel to develop schedules for acoustic activities that take into account the potential for lethal and sub-lethal effects on marine mammal populations.

By using a comparative framework incorporating observed behavioral responses to oceanic noise we will provide several tools for other investigators including, 1) stroking costs for different sized cetaceans for free-ranging energetic evaluations, 2) specific behavioral and physiological risk factors

for establishment of 3-D geographic/oceanic safety zones, and 3) the development of SDSV and PCAD models that will enable us to make more definitive links between individual species vulnerabilities, population dynamics of diving marine mammals and acoustic disturbances in oceans. In this way the proposed study will produce a dynamic product framework that can be modified as new data and information becomes available with future studies.

RELATED PROJECTS

None

PUBLICATIONS

Terrie M. Williams, Lee A. Fuiman, and Randall W. Davis (2015) Locomotion and the cost of hunting in large, stealthy marine carnivores. **Integrative and Comparative Biology**: doi:10.1093/icb/icv025. [published, refereed]

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Terrie M. Williams, Penni Bengtson, Diana L. Steller, Donald A. Croll, and Randall W. Davis (2015) The Healthy Heart: Lessons from Nature's Elite Athletes. *Physiology* doi:10.1152/physiol.00017.2015. [published, refereed]